Revista Ceres, 29(163):296-314. 1982.

ACCESSORY CHROMOSOMES IN PLANTS [1]

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1. INTRODUCTION

The genomes of certain organisms include accessory, supernumerary, or B-type chromosomes in addition to the normal regular diploid chromosomal complement. These chromosomes are of uncertain origin, are inherited in an irregular fashion and are generally held to have little genetic activity.

The first report of supernumerary chromosomes was by WILSON (*102*) who observed them in insect species in the genus *Metapedius*. In 1911, KUWADA (*49*) reported a variable chromosome number in the plant, *Zea mays*. Later, several investigators (*46, 50, 53*) concluded that 10 is the basic number in *Zea* but that other chromosome numbers do occur. LONGLEY (*54*), however, was the first to distinguish the supernumerary chromosome from members of the basic complement of 10. This observation was confirmed by RANDOLPH (*76*), who proposed the designation «B chromosomes» (*77*) and suggested that the normal set be called the A set.

Since then intensive investigations have been carried out in many plant and animal species on the occurrence and behavior of the B chromosomes.

According to a recent survey by JONES (*42*), B chromosomes are found in 591 species in 219 genera of flowering plants, six of which are gymnosperms and the rest angiosperms. Among the families represented, the Graminaceae and Compositae have the largest number of species with B chromosomes. In the animal kingdom, B chromosomes have been described in 116 species (*42*), occurring mainly in insect species in the orders Orthoptera and Coleoptera. In mammals, only six species are known to carry accessory chromosomes (*42*).

Although B chromosomes are not alike in all species they share several characteristics in common. From the reviews on B chromosomes by BATTAGLIA (*10*), JONES (*42*) and MUNTZING (*69*), the following generalizations can be drawn:

1 — They are not essential for normal growth, development and reproduction;

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2 — They are not homologous with the chromosomes of the basic set (A chromosomes);

3 — They carry no genes with major effects since their presence, at least in low numbers, does not modify the morphological characteristics of the organism;

4 — They are often highly heterochromatic and smaller than A chromosomes;

5 — They are unstable at meiosis and/or mitosis and their inheritance is consequently irregular and non-Mendelinan. To compensate for this disadvantage, they have evolved mechanisms of accumulation which insure their persistence in the population.

The above features characterize a typical B chromosome but not all of them are necessarily present in the B chromosomes of every species.

Since B chromosomes are not essential for the survival of the organism and carry no known genes, it is impossible to determine from morphology alone whether or not an individual carries accessory chromosomes. The lack of phenotypic effect led to the belief that they were genetically inert (*71*). Subsequently, however, it became evident that all B chromosomes were not devoid of genetic activity.

Since B chromosomes persist in natural populations, DARLINGTON and THOMAS (*27*) and DARLINGTON and UPCOTT (*28*) concluded that they are useful to the plant. They failed to consider the possibility, now shown to be true, that B chromosomes have accumulation mechanisms which ensure their perpetuation even when they have a dysgenic effect.

OSTERGREN (*71, 72*) suggested that B chromosomes lead a parasitic existence, that they are not beneficial to the host, and that their genetic activity is confined to those cellular activities which ensure their perpetuation. They are relatively harmless when present in low numbers.

Although no critical evidence exists, many geneticists feel that B chromosomes probably are of adaptive significance for no reason other than their persistence in wild populations. Any generalization about the benefits conferred by B chromosomes is fraught with danger because there is no reason to believe that the B chromosomes found in different plants and animals are alike in their genetic effects. Some B's may be deleterious, others neutral or even beneficial.

B chromosomes are responsible for, or participate in, several cellular effects. They are able to alter chiasma frequency and, in maize, increase recombination; they increase DNA and histone contents; and, they are involved in breakage and loss of knobbed A chromosomes in maize (high-loss phenomenon). The presence of B chromosomes is not always associated with obvious effects on the organism; however, when present in high numbers their phenotypic effects are usually deleterious.

2. EFFECT OF B CHROMOSOMES ON CHIASMA FREQUENCY AND RECOMBINATION

According to DARLINGTON (*26*), the beneficial role of B chromosomes involves the increase of genetic variability. B chromosomes may exert an influence upon the genetic variability of populations in an indirect way. MOSS (*63*) found that the presence of B chromosomes in the parents increases the phenotypic variability in their progenies. A possible mechanism is by the control of the distribution and frequency of chiasmata and, consequently, in the amount of genetic recombination at meiosis (*43*). That B chromosomes can influence

chiasma frequency and distribution and the percentage of recombination has been shown in many organisms.

BARKER (*7*) found that B chromosomes raise the chiasma frequency in the A chromosomes of natural populations of grasshoppers. Conversely, B chromosomes have been reported to reduce chiasma frequency in *Triticum speltoides* (*94*), *Lolium* (*19*) and pearl millet (*74*). However, in *Lolium* and pearl millet the B's increase the variance of chiasma frequency.

Although JONES and REES (*43*) found no influence of the B's on mean chiasma frequencies in cultivated populations of rye, they reported a modification in the distribution of chiasmata and an increase in chiasma variation in A chromosomes. Converse results were obtained by ZECEVIC and PAUNOVIC (*103*) in their analysis of two wild populations of rye where the B's increased the mean chiasma frequency. They also reported a dosage effect in plants with different numbers of B's. *Zea mays* is another species in which B chromosomes increase chiasma frequency and variance (*3, 100*). In *Puschkinia libanotica*, the B chromosomes increase chiasma frequency, cause redistribution of chiasmata but reduce the variance of chiasma frequency (*8, 9*).

Thus, the effect of B chromosomes on chiasma frequency is a complicated one. Depending upon the species, the B chromosomes can increase, reduce, or have no effect on the frequency of chiasmata.

The first report of the effect of B chromosomes on genetic recombination was made by HANSON (*35*) in corn. He observed that in the presence of six to nine B chromosomes, crossing over was increased in a proximal region in the short arm of chromosome 9. The effect was manifested primarily in the double and triple crossover classes. The increase in the proximal region was accompanied by a reduction in a distal region. Later, HANSON (*36*) showed an additive effect of B chromosomes in increasing recombination between four markers in chromosome 3.

NEL (*70*) found that higher numbers of B's gave progressively higher crossover values in the proximal segments of chromosome 5 of maize. In the male meiocytes the increase was greater than in the female. For a proximal region of chromosome 9, the B chromosomes caused a slight increase in male flowers which was accompanied by a decreased in the adjacent distal region.

In the maize experiments reported above, the increases in recombination caused by B chromosomes were slight. A major effect occurred in an exceptional case described by RHOADES (*81*). He studied recombination in maize plants homozygous for a transposition (Tp9) in which an interstitial piece from the long arm of chromosome 3 was inserted into the short arm of chromosome 9 between the *C* (aleurone color) and *Wx* (starchy endosperm) loci. In the presence of a single B chromosome, the amount of recombination between these flanking markers was more than double. The data also indicated a slight but significant dosage effect with increasing numbers of B's. However, the increase in recombination was correlated with a reduction in crossing over in the adjacent *Yg-C* region (Yg-green seedling and plant.), indicating a shift in the distribution of crossovers along the chromosome arm.

Using a series of translocations between A and B chromosomes, in which different amounts of B heterochromatin are carried by the A^B translocated chromosome, WARD (*98*) tried to identify the region or segment of the B responsible for the increased crossing over. He found that no specific region of the B chromosome had an exclusive role in the promotion of recombination. With the exception of the distal euchromatic tip of the long arm, all tested segments increased recombination.

CHANG and KIKUDOME (*23*) reported that maize plants with odd numbers of B chromosomes had higher crossover values for chromosome 9 in megasporocytes than did those with even numbers.

That enhancement of crossing over by B chromosomes is not confined to intergenic recombination was demonstrated by MELNYCZENKO (*60*), who found that one or two B chromosomes caused an increase in intragenic recombination in maize, between alleles at the waxy locus.

So far, the effect of B chromosomes on genetic recombination has been studied only in maize. This undoubledly reflects the availability of large numbers of easily scored endosperm genes in this species.

Unresolved is the question whether the effect of B chromosomes on genetic recombination and chiasma frequency are achieved through their influence on chromosome pairing at or prior to pachytene or upon other events subsequent to pairing. That B chromosomes can, however, influence the pairing process was showed by EVANS and MACEFIELD (*30*) in *Lolium*.

It has been suggested that B chromosomes produce genetic variability because of their influence on chiasma frequencies and genetic recombination and that this greater variability may be of adaptive significance in certain natural environments (*74*). However, RHOADES and DEMPSEY (*84*) argue that the effect of B's on recombination and chiasma may be indirect, stemming from a lengthening of the cell cycle. The argument that B's confer a beneficial effect by increasing recombination becomes suspect if the increase in one region is accompanied by a decrease in other regions, i.e., if B's cause a redistribution of chiasmata but not necessarily an increase in the total amount of crossing over. It is possible that B's enhance recombination in proximal heterochromatic regions, which have low crossing over per unit length, and consequently break up the linkage between tightly clustered genes; but, if true, this would be at the expense of genic recombination in the euchromatic portions of the chromosome. The net advantage of increased variance may be slight. What is needed is a study of crossing over where the entire arm is marked.

3. PHENOTYPIC EFFECTS

The primary evidence that B chromosomes of maize are genetically inert came from the work by RANDOLPH (*78*). By genetic tests of genes distributed among 17 of the 20 arms of the A chromosomes, he found that these alleles were not represented in the B chromosomes. Moreover, he did not observe any visible phenotypic differences in plants possessing as many as 10 B's. Supporting the inert hypothesis is the fact that in maize, and indeed in most species, the B chromosomes consist chiefly of heterochromatin. Heterochromatin is known to be genetically inert since there is no RNA transcription and no or only a few active genes are in the heterochromatin (*18*). The inertness of heterochromatin is also demonstrated by the fact that gross deficiencies of heterochromatic segments are tolerated by the organism; they produce no phenotypic change. In contrast, small deletions of euchromatin are often lethal to the organism (*82*).

DARLINGTON (*26*) and MATHER (*56*) speculate that the DNA of the B chromosomes consists of polygenes, which have small and less specific effects and are believed to be responsible for quantitative variation. According to this hypothesis, the B chromosomes would be active, the apparent inertness ascribable to the absense of major genes. Possessing only genes with minor effects, the role of B chromosomes in growth and development would be difficult to detect.

Although the data from diverse organisms are contradictory, the bulk of the evidence suggests that B chromosomes are not truly inert organelles. They apparently can produce changes of a quantitative nature which may or may not be of benefit to the host. There is no reason to believe that B's in different species are alike and this may account for the divergent findings and conclusions regarding the function and genetic activity of B chromosomes. However, it appears that most, perhaps all, of the phenotypic effects ascribed to B chromosomes are of a quantitative rather than a qualitative nature.

In some species, e.g., *Tradescantia*, the B chromosomes produce no detectable phenotypic changes irrespective of the number of B's (*2*), while in others, modifications arise with high numbers of B's. RANDOLPH (*78*) could find no effects of low number of B's in maize but when the number of B's became high (from 10-15 and more) there was: (a) a reduction in fertility; (b) decreased vigor; (c) production of defective seeds that are frequently germless or have a partially developed endosperm; (d) scarred endosperm; (e) an increase in nuclear and cell size; and, (f) variation in pollen size and an increase in the percentage of aborted pollen grains. Later, KATO (*45*) found that increasing the number of B chromosomes produced corn plants with delayed anthesis which were also shorter in height. Recently, McGIRR and ENDRIZZI (*58*) tested the reaction to viral infection of maize plants with and without B chromosomes. Plants with and without B's showed no significant difference in susceptibility to Brome Mosaic Virus or to Maize Dwarf Mosaic Virus. They found, however, a slight but significant difference in susceptibility to Wheat Streak Mosaic Virus with respect to the time of systemic necrosis. Plants with one or two B chromosomes were later in developing leaf necrosis than were those lacking B's. One criticism of this work is that they used plants with only one or two B chromosomes. It would be of interest to determine the resistance to leaf necrosis in plants with higher numbers of B's — i.e., to ascertain if there is a dosage effect.

In contradistinction to the evidence presented earlier purporting to show that the B chromosomes of rye benefit their carriers, there are investigations where B's proved to be deleterious.

MUNTZING (*64, 65*) found that B chromosomes have a negative effect on kernel weight per plant, on number of kernels per ear, on percentage of seed set, and on pollen fertility. However, a decrease in straw weight, plant height and number of culms could only be demonstrated when at least four B's were present. All of these negative effects of B chromosomes in diploid rye were also observed by MUNTZING (*67*) in a tetraploid strain indicating that the effect of B chromosomes does not depend upon the ratio between the number of A chromosomes and the number of B chromosomes, and also supporting the view that genes in the normal chromosomes of rye are not represented in the B chromosomes. An interesting observation by JONES and REES (*44*) with rye showed a zig-zag relationship between certain phenotypic characters (plant weight, tiller number and straw weight) and alternating odd and even numbers of B's with the odd numbers of B's giving lower phenotypic scores. B chromosomes of rye when transferred to a wheat strain also reduced pollen fertility and female fertility (*68*).

In *Trilium grandiflorum*, seed fertility was favourably influenced by the introduction of up to three B chromosomes (*93*). Since the B chromosome in this species is euchromatic and presumably has active genes one would predict and adverse rather than a favorable response to the addition of B's.

B chromosomes reduce seed and pollen fertility in *Lilium callosum* (*47*) and in *Collinsia* (*29*), pollen fertility and growth in *Aegilops speltoides* (*61*), fertility and seed yield in crested wheatgrass (*6*) and fertility in pearl millet (*74*).

In *Festuca pratensis* (*16*) and *Centaurea scabiosa* (*32*), only high numbers of B's

have a negative effect on vegetative development as well as on fertility. One plant with 22 B chromosomes in *Centaurea scabiosa* still had 75% of good pollen. Small numbers of B chromosomes had variable effects on fertility and vegetative development. This led BOSEMARK (*17*) to suggest that the genetic effect of low number of B's in *Festuca pratensis*, and probably other species as well, is partly governed by the genotypic constitution of the organism and partially by the prevailing environmental conditions.

MEHRA and MANN (*59*) observed that B chromosomes in *Pterotheca falconeri* had a deleterious effect on vegetative growth, pollen and seed fertility. The presence of only one B gave plants shorter in height and with smaller leaves; plants with two or three B's appeared dwarf. Thus, in this specific case, the presence of B chromosomes could be detected phenotypically. Since this species is characterized by a low number of basic chromosomes (n = 3), it seems that the addition of a single B has an appreciable deleterious effect.

Only two cases have been reported where B chromosomes have been claimed to be associated with a specific plant character. In *Haplopappus gracilis* (*39*), plants containing B chromosomes could be distinguished by certain morphological characteristics of the leaves and stems. In addition, the achene coats of plants with accessory chromosomes were found to be a dark red color while plants without B's was usually brown. JACKSON and PHILIP (*40*) found that addition of one, two and four B chromosomes to the basic complement was accompanied by an increase in the amount of one type of pigment in the achene walls. Although addition of three B's produced less pigment than plants with one or two B's, the data suggests that the B chromosomes carry genes for pigment production which are similar to, or the same as, those on the normal chromosome. Since this species has an unusually low number of A chromosomes (n=2), it is possible here, as in *Pterotheca falconeri*, that the proportion of B chromosome-DNA in the nucleus is sufficiently high that any of its potential genetic effects are not swamped by the activity of genes in the A set. A difference between the two organisms is that the B's had a deleterious effect in *Pterotheca falconeri* but not in *Haplopappus gracilis*.

PALIWAL and HYDE (*73*) found male sterility associated with a B chromosome in *Plantago coronopus*, but their evidence does not conclusively place the male sterility factor on the accessory chromosome.

4. HIGH-LOSS PHENOMENON

RHOADES *et alii* (*87*) discovered, in maize, an unexpected and dramatic effect which results from the interaction of B chromosomes with the heterochromatic knobs of the A chromosomes. The «high-loss phenomenon» is characterized by breaks in knob-bearing chromosomes and the consequent loss of the acentric portion of the chromosome arm distal to the breakpoint. Breaks are induced in knobbed chromosomes at the second microspore division only when at least two B chromosomes are present.

RHOADES *et alii* (*87*) demonstrated that high-loss is controlled by B chromosomes. When corn plants containing several B chromosomes and carrying the dominant markers, Al (anthocyanin) and *Sh2* (nonshrunken endosperm), *in* chromosome 3, were used as males in crosses with *al sh2* testers, the frequency of loss was as high as 20%. However, the reciprocal crosses, in which plants with B chromosomes and dominant alleles were used as female parents, gave no loss. Similarly, no loss was observed in related plants without B chromosomes. The stock in which loss occurred was designated the «high-loss line».

Cytological analysis of high-loss plants showed that chromosome 3 was homozygous for a large knob on the long arm. The importance of the knob in the high-loss phenomenon was demonstrated using a high-loss derivative knobless for chromosome 3. In the absence of the knob, no loss of chromosome 3 markers occurred. Thus, the high-loss phenomenon requires an interaction between B chromosomes and the heterochromatic knobs on A chromosomes.

The high-loss phenomenon is not restricted to the knob of chromosome 3. Knobs of chromosomes 4, 5, 9, and 10 also interact with B's to give chromatin elimination (*84, 85*). RHOADES and DEMPSEY (*84, 85*) concluded that all knobbed chromosomes are subject to loss in the presence of B chromosomes. Additional observations revealed that larger knobs undergo loss more frequently than smaller ones.

A study of the effect of different numbers of B's showed no evidence of a dosage effect since plants with four to eight B's gave no marked differences in the frequency of chromatin elimination, while plants with one or two B's gave negligible loss (*84*). The conclusion is that chromatin loss frequently occurs in microspores with at leást two B chromosomes, but there is no dosage effect with additional B's.

B chromosomes of different strains of maize are able to induce loss from knobbed A chromosomes at the second microspore division (*83*). However, genetic modifiers can markedly affect the rate of loss. Two sister plants, each possessing a knobbed chromosome 3 and six B chromosomes, gave 9.2% and 3.5% loss of the A marker. Stock without the background genes of the high-loss strain showed no knob-B interaction (*84*). Thus, although knobs and B's are essential for chromatin elimination, their potential to produce loss is controlled by modifying genes.

RHOADES *et alii* (*87*) observed that crosses of *a1* female testers with high-loss males homozygous for *A1* gave exceptional *a1* kernels exhibiting loss of the *A1* allele in the endosperm. When planted, these kernels gave rise to plants carrying the dominant allele. The noncorrespondence between the embryo and endosperm constitutions indicates that some pollen grains of the high-loss parent contained dissimilar sperm and that the mitotic division producing the two sperm nuclei must be the stage at which loss occurs. Thus, the high-loss phenomenon takes place at the same division in which B chromosomes undergo nondisjunction, namely the second microspore mitosis. Although both phenomena occur at the same division, B chromosomes and deficient A chromosomes assort independently at the second microspore divìsion (*84*).

The presence of the knob is required for loss and the position of the knob, with respect to the markers followed, determines the pattern of loss. Two patterns have been identified genetically by examining endosperm phenotypes (*84, 85*). Pattern I was described for markers on chromosomes 4, 5, 9, and 10; in all instances, the dominant gene lay between the knob and the centromere. Endosperm from pattern I loss may exhibit either a completely recessive phenotype or a mosaic phenotype combining the dominant and recessive traits. Breaks in the knobbed chromosome between the marker gene and the centromere will produce a deficient chromosome lacking the dominant gene. If this chromosome fertilizes the polar nuclei, the resulting endosperm has a wholly recessive phenotype. Breaks between the marker gene and the knob give a deficient chromosome with the dominant marker. If this chromosome is in the endosperm, it undergoes a bridge-breakage-fusion cycle and produces kernels mosaic for dominant and recessive tissue. On the other hand, loss events of pattern II lead to whole loss only. Patern II was observed in studies with chromosome 3 possessing an endosperm marker gene distal to the knob; the exceptional kernels were

completely recessive and no mosaic kernels were found.

The association of a specific loss pattern with a particular arrangement of the knob, marker gene, and centromere led RHOADES and DEMPSEY (*84, 85*) to propose a mechanism to account for chromatin loss. According to their hypothesis, B chromosomes induce a delayed replication of the knobs at the second microspore division resulting in a dicentric bridge at anaphase. Breakage of the bridge between the knob and centromere produces deficient chromosomes and the type of loss pattern will depend on the location of the marker gene.

One test of the validity of the hypothesis is to determine the loss pattern for an inverted chromosome 3 (In 3a) in which the marker gene is situated between the knob and the centromere instead of lying distal to the knob as is the case for a normal 3. RHOADES and DEMPSEY (*85*) found that high-loss knobbed plants with the inverted chromosome 3 gave both whole loss and mosaic kernels as predicted.

Although breaks can occur anywhere between the knob and the centromere, the distribution of breakpoints in the postulated dicentric bridge is nonrandom (*85, 86*). This was clearly illustrated in studies involving a chromosome 9 carrying a large knob at the end of the short arm. Two endosperm marker genes in 9S were followed; the *Wx* locus lies approximately in the middle of the short arm and *C* is closer to the tip with a cytological position of about 0.75 (*57*). RHOADES and DEMPSEY (*85*) found that 91% of the breaks occurred in the centromere-Wx region, while about half of the remainder occurred between the *Wx* and *C* loci, and the other half between *C* and the end of the short arm. Consequently, there is a high probability of breakage of the dicentric bridge in the proximal, deeply-staining half of the short arm. The tendency toward preferential breakage in the proximal segments, and especially at the centromere region, was noted in other knobbed chromosomes and Rhoades and Dempsey concluded that the junction of the chromosome arm with its centromere is a particularly weak site.

Unfortunately, Rhoades and Dempsey were unable to demonstrate cytologically the anaphase bridges at the second microspore mitosis postulated in their hypothesis. At this stage the microspores are surrounded by a thick exine layer and the cytoplasm contains numerous starch granules; these factors have made the visualization of the loss mechanism technically difficult.

5. POSTMEIOTIC NONDISJUNCTION

Since B chromosomes have developed efficient mechanisms of accumulation in different species, they can be maintained in populations even if they are not useful to the organism.

The most common type of an accumulation mechanism leading to numerical increase is that of postmeiotic nondisjunction. This mechanism has been extensively studied, especially in maize and rye.

LONGLEY (*54*) first reported the irregular inheritance of the B chromosome of maize and suggested that it undergoes nondisjunction. However, RANDOLPH's (*78*) more extensive experiments disclosed that reciprocal crosses between plants with and without B chromosomes differ with respect to the frequency distribution of plants with various numbers of B's in the progeny. Since the expected results were obtained when the B's were transmitted by the seed parent, but not by the male parent, he proposed that B's underwent some type of anomalous behavior during the division of the generative nucleus to form the two male sperm.

ROMAN (*90*) used translocations between B and A chromosomes to study the

anomalous transmissional behavior of the B chromosome. He reasoned that if mitotic nondisjunction of the B chromosome occurs in the first division of the microspore then the two gametes within a pollen grain would be identical with respect to B chromosome number while nondisjunction at the second microspore division would produce two dissimilar sperm cells. Since one sperm fertilizes the egg to form the embryo and the other the polar nuclei to form the endosperm the production of dissimilar sperms would lead to nonconcordant constitutions of the embryo and endosperm in terms of B chromosomes contributed by the male parent. The results of crosses involving plants homozygous for the TB-4a translocation, in which the fate of B^4 translocated chromosome with its segment from 4S carrying the *Su* allele (nonsugary endosperm) can be followed by its effect on the endosperm, demonstrated that the B^4 chromosome, possessing the centromere and proximal third of the B chromosome and the distal three fourths of the short arm of chromosome 4, undergoes nondisjunction at the second microspore division while the 4^B chromosome does not. As a consequence, the two gametes of a pollen grain carry different chromosomal complements. One has the B^4 chromosome in duplicate; the other is deficient for this chromosome, but both sperm cells function in fertilization.

As the consequence of nondisjunction of the B^4 chromosome at the second microspore mitosis, one of the sperm has two B^4 and one 4^B chromosomes while the sib sperm has no B^4 and one 4^B. The two dissimilar sperms in the same pollen grain do not randomly fertilize the gametic nuclei of the embryo sac. The hyperploid ($B^4B^4{}_4B$) sperm preferentially fertilizes the egg while the hypoploid (4^B) sperm unites with the polar nuclei — i.e., there is preferential fertilization. Crosses involving intact B's showed that sperm hyperploid for B's preferentially fertilized the egg (*91*). Both the intact B's and the B^A chromosome confer on sperm the ability to preferentially fertilize the egg (*20, 21, 22*).

Nondisjunction of the B^4 chromosome in 4^BB^4 microspores occurred with a frequency as high as 80% (*92*). However if the 4^B chromosome was not present in the microspore, the B^4 chromosome did not undergo nondisjunction. Thus, although the 4^B chromosome itself disjoins normally at the second microspore division, it controls nondisjunction of the B^4 chromosome.

BLACKWOOD (*12*) found that the rate of nondisjunction is not a constant; different rates of nondisjunction occur during the second pollen grain division.

The investigations delineated above show that the B chromosome of maize undergoes nondisjunction at the second microspore division and that this is followed by preferential fertilization of the egg by hyperploid sperm. Nondisjunction at the second microspore in conjunction with preferential fertilization of the egg pronucleus by the hyperploid sperm provide the mechanism which ensures the maintenance of the B chromosomes in the population.

Roman's observation that the 4^B chromosome is essential for nondisjunction of the B^4 chromosome shows that the distal two-thirds of the B chromosome, that portion borne by the 4^B chromosome, controls nondisjunction. WARD (*99*) succeeded in further localizing the site of the controlling element in his analysis of the TB-8 translocation where he clearly demonstrated that it lies in the short euchromatic tip of the long arm of the B. The B^8 chromosome has all of the chromatin of B except the short terminal euchromatic segment which consists of two chromomeres. Nondisjunction of the B^8 chromosome in 8^BB^8 microspores occurred with a frequency greater than 90%, while there was no nondisjunction of B^8 in $8B^8$ microspores. Thus, the site controlling B nondisjunction is located in the distal euchromatic tip of the long arm.

Recently, LIN (*52*) claimed that a region in the proximal euchromatic portion

of the B is also involved in nondisjunction.

The B chromosome of maize characteristically nondisjoins with high frequency at the second microspore division but it can sporadically and rarely undergoes nondisjunction at other divisions. BLACKWOOD (*12*) observed nondisjunction of the B chromosome at anaphase I of meiosis in pollen mother cells and BIANCHI *et alii* (*11*) and CARLSON (*20*) attributed sectored losses in both the endosperm and sporophyte tissues to nondisjunction of B^A chromosome.

Nondisjunction of B chromosome also occurs in rye, but the mechanism does not operate at the second microspore division, but in the first one. HASEGAWA (*37*) first observed that nondisjunction of the B chromosome in rye occurred at the first pollen mitosis and that the two nondisjoined chromatids preferentially were included in the generative nucleus. Later, MUNTZING (*65*) showed that directed nondisjunction also occurs on the female side, and HAKANSSON (*33*) observed cytologically that it took place at the first division in the embryo sac. MUNTZING (*66*), in his detailed cytological studies on the mechanism of nondisjunction at the pollen mitosis in rye, observed that at anaphase the centromere has divided and the sister centromeres move to opposite poles. However, resistance to anaphase separation occurs because of the «stickness» of two putative heterochromatic regions, one in each arm. The conjoined chromatids in most cases pass to the generative pole. Separation of the conjoined chromatids occurs during the interphase between the first and second mitosis. HAKANSSON (*34*) reported that a B chromosome deficient for the terminal half of the long arm could not induce nondisjunction. However, LIMA-de-FARIA (*51*) found that the deficient B is able to undergo nondisjunction when a standard B chromosome is present in the same microspore, and concluded that the knob region of the standard B is responsible for the delayed reproduction of the two segments of the deficient chromosome that prevents anaphase separation. Essentially the same situation was described by BOSEMARK (*14*) in *Festuca pratensis*. Although the segment missing in the deficient B chromosome of rye includes not only a large knob but also the terminal appendage and a thin 'neck region', MUNTZING (*69*) concluded that the nondisjunction is conditioned by the large knob. It was postulated to secrete a chemical substance that affects the chromatids of the defective B in some manner as to inhibit normal separation. However, we can recall that in maize, although the B chromosome is highly heterochromatic, the site(s) that controls nondisjunction is located in the distal two euchromatic chromomeres.

It is possible that the mechanism of B nondisjunction in *Collinsia* is similar to that in rye. DHILLON and GARBER (*29*) observed that the number of B chromosomes increases during the formation of both male and female gametes. However, it is not known at which postmeiotic mitosis nondisjunction occurs, but they observed that meiosis was normal.

The mechanism of B chromosome nondisjunction in sorghum is unique. DARLINGTON and THOMAS (*27*) observed no abnormal behavior in plants with B's at the first microspore division. However the vegetative nucleus rapidly undergoes one or more extra divisions (polymitosis), giving rise to additional generative nuclei. At each extra division, the B's pass undivided to the generative pole and so double its dose. When only two generative nuclei are formed, one or both may produce sperm. However, three, four or five generative nuclei result in lethality.

In a number of plant species, B chromosomes have the restricted ability to undergo oriented postmeiotic nondisjunction only to the generative nucleus at the first pollen mitosis. This mechanism has been described in *Anthoxanthum aristatum* (*72*), *Festuca pratensis* (*13*), *Phleum phleoides* (*15*), *Festuca arundinacea, Briza media, Holcus lanatus* and *Alopecurus pratensis* (*17*), crested

wheatgrass (*5*), *Dactylis hybrids* (*101*), *Dactylis glomerata* (*75*) and *Aegilops speltoides* (*61*), and others.

Although postmeiotic nondisjunction is the most characteristic accumulation mechanism of B chromosomes in plants, it is, however, limited to the grass family. The following different and less known mechanisms are supposed to occur: (a) somatic nondisjunction; (b) meiotic preferential distribution; and, (c) endomitotic reduplication.

6. MOLECULAR ANALYSIS

For a better understanding of the function and origin of B chromosomes, molecular genetic analysis is of fundamental importance. So far, this kind of investigation has been limited to a few species. Some of the results obtained are as follows.

RINEHART (*89*) found that DNA from maize, with and without B chromosomes, band at the same place. There is no minor peak, B chromosome DNA having an overall G-C content of 42%, the same as the DNA from A chromosomes. ABRAHAM and SMITH (*1*) observed that the B chromosomes of maize, as is true of constitutive heterochromatin in a generic sense, synthesize DNA during the last half of the S period.

HIMES (*38*) compared interphase chromatin of maize having no B's with that of maize with approximately 20 B chromosomes. She concluded that B chromosomes increase the DNA and histone content, although they are maintained in the same proportion; and, that an increase in the nuclear volume was produced by the B's but they did not synthesize chromosomal RNA.

CHILTON and McCARTHY (*24*) observed that DNA preparations from maize seedlings without B and with five B's were indistinguishble in buoyant density CsCl gradients, general renaturation kinetics, or melting behavior of renatured duplexes. However, they pointed out that with the number of B chromosomes used it would be very difficult to detect any difference unless B-DNA were very unusual or differed grossly from A-DNA.

Studies have also been conducted with *Secale cereale* on the constitution of the B chromosomes at the molecular level. AYONOADU and REES (*4*) found that the duration of the mitotic cycle in root tips of rye is increased by the presence of B chromosomes. This is also true for *Zea mays* and *Lolium perenne* (*80*). This increase in the duration of mitosis together with the increase in cell size, as observed in *Secale cereale* (*41*), could explain some of the phenotypic consequences of DNA variation due to B chromosomes.

The B chromosomes of rye increase the amount of nuclear DNA and histone protein but decrease the relative amount of total nuclear protein and nuclear RNA (*48*). They (*48*) observed that the increase in histone was disproportionately high in plants with odd numbers of B's whereas the decrease in protein and RNA content was disproportionately low in the same odd numbered plants. This odd and even phenomenon seems to have a counterpart at the organism level, since there is a relationship between odd and even numbers of B chromosomes and phenotypic expression (*44*). In rye, the B's increase the histone/DNA ratio; this differs from maize where this ratio is constant (*38*). However maize data are from newly germinated roots whereas rye data come from secondary roots. In rye, in plants with B's there was no disproportionate increase in any single class of histone, rather there was a general increase in all of the fractions (*41*). The increase of histone protein by B chromosomes may affect gene action since it has been

claimed that gene expression is negatively correlated with histone concentration. The argument is that there is a non-specific attachment of histones to the chromosomal DNA and a consequent repression of gene activity (*18*).

RIMPAU and FLAVELL (*88*) found that the proportion of repeated sequences in the DNA's of the A and B chromosomes was similar, indicating that the DNA of the A and B chromosomes of rye do not differ greatly.

The molecular analysis of the B chromosomes in maize and rye showed that there is a strong similarity between A and B chromosomes in base composition.

7. ORIGIN

The origin of B chromosomes in plant species has been a subject of much speculation and although no clear conclusion has been reached it is generally accepted that B chromosome is of ancient origin.

The molecular analysis of B chromosomes in maize and rye show that the DNA of A and B chromosomes is similar in base composition. This suggests, but does not prove, that B chromosomes originated from A chromosomes. However, the lack of pairing at meiosis, indicative of little homology between A and B chromosomes, has been frequently used to argue against this relationship, although the possibility exists that in the distant past some kind of structural rearrangement or heterochromatization took place which would preclude synapsis.

In maize it has been suggested that there is a relationship between B chromosome and the abnormal chromosome 10(K10), which carries an extra piece of chromatin including a large heterochromatic knob. TING (*97*) proposed that a translocation between chromosome 10 and a B chromosome gave rise to K10 chromosome. However, SNOPE (*95*) found in haploid maize that there was no bivalent formation involving single B and K10 chromosomes even though the haploid nature of the pollen mother cells provides the maximum opportunity for pairing between chromosomes showing homologous sequences, however short they may be.

REES (*79*) proposed that B chromosomes evolved from A chromosomes, and accounts for the absence of homology between A and B chromosomes at meiosis by assuming that the composition and organization of B-DNA have diverged substantially from that of the original A chromosome fragments.

RIMPAU and FLAVELL (*88*) proposed that in rye the DNA of the B chromosome originated from that of an A chromosome by fragmentation. Supporting this suggestion was the finding of rRNA genes on one of the two types of rye B chromosome tested (*31*). This result led to two conclusions: (1) Not all B chromosomes in rye are identical; (2) The B chromosome with rRNA genes must have originated by fragmentation of the member of the A set which carries the nucleolar organizer region while the other type of B came from different segments of the A. However, pairing would be expected between the A chromosome with the nucleolus organizer region and one of the two kinds of B chromosomes but this has not been reported.

However, in a few plants, pairing and even chiasmata between A and B chromosomes have been observed, pointing more directly to the origin of their B's from A chromosomes. MEYER (*62*) observed chiasma between B chromosome and centromeric region of major chromosomes in *Phlox* and suggested that in this species the B chromosome arose by the loss of the distal portions of the A chromosomes. Breakage of inversion bridges at meiosis, which are common in this species, was the mechanism by which loss of distal regions was postulated to occur.

The B chromosome in *Tradescantia* is small and heterochromatic. DARLINGTON (*25*) observed pairing of B's with terminal or centric regions of A chromosomes. According to SWANSON (*96*), the end pairing is specific but the centric pairing may not be. The observed pairing supports Darlington's hypothesis that the B chromosome is homologous with one or more of the A chromosomes and that the homologous portions are at the distal and proximal regions of the chromosome arms. Swanson suggests that diminution of chromatin can result from several processes: intercalary deletion; overlapping inversions; and, translocations. Similar cases of pairing and chiasmata between the B chromosome and segments of A chromosomes have been reported in *Lilium henrye* and *Lilium japonicum* (*55*).

8. SUMMARY

In addition to the normal regular diploid chromosomal complement, the genones of many plant species include accessory chromosomes.

In this article a critical review is presented as to the effect of the accessory chromosomes upon recombination between genes on chromosomes of the regular set; the phenotypic effects; and, a detailed analysis of the high-loss phenomenon. Also examined are the following aspects related to the accessory chromosomes: postmeiotic nondisjunction; molecular analysis; and, origin.

9. RESUMO

Muitas espécies de plantas possuem, além dos cromossomos do complemento diplóide normal, cromossomos acessórios.

Estudam-se, neste trabalho, os efeitos dos cromossomos acessórios sobre a porcentagem de recombinação de genes localizados em cromossomos do complemento regular e os efeitos fenotípicos causados pela presença dos cromossomos acessórios, bem como analisa-se minuciosamente o fenômeno de indução de quebras cromossômicas. São analisados, ainda, os seguintes aspectos relacionados com os próprios cromossomos acessórios: origem, não-disjunção pós-meiótica e análise molecular.

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